

## The Rhizome Scales of *Platycerium*<sup>1</sup>

BARBARA JOE HOSHIZAKI

Considerable diversity exists in the structure of fern rhizome scales. Although the more conspicuous features of scales have long been used in describing and identifying some groups of ferns, the more detailed aspects have generally been ignored. Modern monographs and treatments on ferns have contributed to a better understanding of the value scales may have in the interpretation of evolutionary relationships. The object of this paper is to describe some of the rhizome scale features of *Platycerium* that seem to be helpful in determining the evolutionary trends within the genus. Some similar features have been pointed out by Wagner (1952, p. 77) in the genus *Diellia*.

Before the rhizome scales could be studied for structures that might be of phylogenetic value, it was necessary to determine first the probable evolution of the *Platycerium* species. For this, I used a variety of characters other than those of the rhizome scales. Reliable characters included stele types, sporangial arrangement, nature of the sporangial stalk, and completeness of the annulus. Only after I had arrived at the probable evolution of the species did I examine the rhizome scales in detail to determine how their features correlated with the patterns I had determined. The three main lines of evolution are summarized in Table I. The Afro-American line includes *P. andinum* and two branches both starting from *P. quadridichotomum*. One branch ends in *P. angolense* and the other branch ends in *P. ellisii*. The sequence of species in the other two lines is essentially linear, as listed.

In selecting rhizome scales for study several factors must be kept in mind. The scales on individual plants vary, but species differences are usually consistent, providing the factors of the age of the plant, weathering, and selection of a typical scale from the sampling are taken into consideration. Immature or small plants

---

<sup>1</sup> Research supported by a National Science Foundation Science Faculty Fellowship.



generally have smaller, lighter, and fewer bicolorous scales bearing fewer hairs than those on mature plants. On fully mature plants scales may have suffered damage by weathering and must be assessed accordingly. The best scales for study are those that are starting to darken on full grown plants. Even in perfect material there will be variations; the largest, darkest scales usually show the characters of the species more clearly than the narrower, smaller, lighter colored scales or fibrils. In regards to selection of trichomes for study, Carlquist (1961, p. 33) aptly states, "Each trichome type in each species shows some variability and thus each type should be studied as a *population* having extremes and a typical condition."

The plants used in this study are from cultivation; for most the specific place of collection is not known.<sup>2</sup> Silhouettes of the scales were made by tracing photographs; drawings of the hairs were made with the aid of a microprojector.

#### MORPHOLOGY AND EVOLUTIONARY SIGNIFICANCE OF SCALES AND THEIR HAIRS

*Scale distribution.*—Rhizome scales are most conspicuous on the buds, but also cover the entire surface of the stout rhizome and extend up the phyllopodia occasionally to just beyond the abscission layer. On the bud the many light colored scales are tightly overlapped and appressed to the surfaces. Progressing to the older parts of the rhizome, the scales become darker, less appressed, and may twist or curl to form a thick, chaffy covering; they are persistent.

*General shape.*—Each plant bears scales of various widths and lengths; the larger, darker scales are here considered the representative scales of a species. For most species these are more or less narrowly triangular. However, the scales of *P. andinum* and *P. angolense* (Figs. 14, 15) are noticeably linear-triangular, and in *P.*

---

<sup>2</sup> Messrs. Ed Franks, Rudy Ziesenhenné, Marcel Lecoufle, and John Roach very generously provided most of the plants and specimens for this study, and I am greatly indebted to them for their many kindnesses. I wish to thank Miss Marie Sanchez for her expert advice in preparing the illustrations and also to acknowledge the assistance and many valuable suggestions given to me by Dr. Mildred E. Mathias. The major part of this work was done at the University of California, Los Angeles, where facilities were kindly provided.



*coronarium* and *P. ridleii* they are obovate (Figs. 29, 30). All but *P. coronarium* and *P. ridleii* have fibrils (very narrow scales) which also vary in width and length on the same plant; the narrowest are uniseriate flattened hairs and the widest are indistin-

TABLE I. SPECIES AND THEIR RHIZOME SCALE CHARACTERS

Character states	Fibrils	Scales		Apex	
		narrow	not	filiform	Base non-
3 = very specialized	present	(0),	papery	(0), acute	peltate
2 = specialized	(0),	(1),	(0),	(1), blunt	(0), sub-
1 = intermediate	absent	broad	papery	(2), round	peltate
0 = generalized	(2)	(2)	(2)	(3)	(2)
AFRO-AMERICAN LINE					
<i>P. andinum</i>	0	0	0	0	0
<i>P. quadridichotomum</i>	0	0	0	0	0
<i>P. stemaria</i>	0	0	0	0	0
<i>P. angolense</i>	0	0	0	0	0
<i>P. madagascariense</i>	0	0	0	0	0
<i>P. vassei</i>	0	0	0	0	0
<i>P. ellisii</i>	0	0	0	0	0
JAVAN-AUSTRALIAN LINE					
<i>P. willinckii</i>	0	0	0	0	1
<i>P. veitchii</i>	0	0	0	0	1
<i>P. bifurcatum</i>	0	0	0	1	2
<i>P. hillii</i>	0	0	0	1	2
MALAYAN-ASIATIC LINE					
<i>P. wallichii</i>	0	0	0	0	0
<i>P. holttumii</i>	0	1	0	2	0
<i>P. wandae</i>	0	1	0	2	0
<i>P. grande</i>	0	2	2	3	0
<i>P. coronarium</i>	2	2	2	3	0
<i>P. ridleii</i>	2	2	2	3	0

guishable from narrow scales. The almost universal presence of fibrils in the genus seems to indicate the ancestral type had fibrils which developed into progressively broader scales. It is generally accepted (Bower, 1923, pp. 201-205) that hairs preceded fibrils and that fibrils developed into scales. Following this line of reasoning,



narrow scales probably gave rise to broad scales. Extremely broad scales (*Figs. 26-30*) seem to be linked to the development of flabelloid margins. The scale length varies from 2 to 35 mm, the longest being those of *P. wandae* and the shortest those of *P.*

<i>Hairs or papillae marginal</i> (0), sub-marginal (1), super-ficial (2)	<i>Special-ized hairs</i> none (0), semi- (1), mostly (2), all spec. (3)	<i>Basic hairs</i> none (0), 1-7-celled (1), 8-celled (2)	<i>Special-ized hairs</i> none or mostly 2-5-celled (0), 1-2 (1), 1 (2)	<i>Partial stellate hairs</i> absent (0), present (2)	<i>Flabelloid margin</i> none (0), narrow (1), intermediate (2), broad (3)	<i>Total value of specialized states</i>
0	2	0	0	2	0	4
0	1	0	0	0	0	1
0	1	0	0	0	0	1
0	2	0	0	2	0	4
0	1	0	0	0	0	1
1	2	0	1	0	0	4
2	3	0	2	0	0	7
0	1	0	0	0	0	2
0	1	0	0	0	0	2
0	1	0	0	0	0	4
0	1	0	0	0	0	4
0	0	0	0	0	0	0
1	0	2	0	0	1	7
1	1	1	0	0	2	8
1	1	0	0	0	2	11
0	3	0	1	0	3	16
1	3	0	2	0	3	18

*willinckii*. The scales on the phyllopodia are larger than those on the rhizome. The texture of the scales is usually firm, but some *P. grande* scales are thin and papery and those of *P. coronarium* and *P. ridleyi* are also except at the center; this is probably a specialized condition.



*Scale apex.*—Scale apices may be long attenuate to acute, to blunt, rounded or emarginate (*Figs. 2-5*). Typically the attenuate apices end in a long, often gland-tipped filament. Acute apices have fewer and stouter cells in the filament; blunt apices are multicellular and sometimes apiculate or emarginate. The apices may often be branched into a number of hairs or filaments. If it is true that scales have been derived from hairs, then the generalized scale apex would be attenuate and filiform and the specialized apex blunt and multicellular. There would be a trend toward increasingly broad apices. There remains, however, the possibility that the extremely long attenuate apices of *P. angolense* and *P. andinum* may be a specialized condition.

In the clear evolutionary line of the Malayan-Asiatic group there is a series from generalized to specialized apices. The intermediate state consists mostly of acute apices that are rarely filiform. The Javan-Australian group has the generalized to intermediate state; the Afro-American group tends to the generalized.

*Scale base.*—The scale base may be slightly narrowed, rounded, truncate, or subcordate to cordate (*Figs. 9-13*); however, most are unmodified. Most scales are sessile and attached by the length of their basal edge (*Fig. 9*), which may be a broadened area if the scale is bent and appressed to the rhizome (*Fig. 10*). Scales may also be subpeltate (pseudopeltate) to peltate. In all cases the scales interrupt the rhizome epidermis at their point of attachment. The subpeltate condition (*Fig. 12*), found on some scales of *P. willinckii*, *P. veitchii*, and *P. bifurcatum*, is often accompanied by a subcordate or cordate base; the attaching tissue is a long or short flange. *Platynerium hillii* and some forms of *P. bifurcatum* have weakly peltate scales with rounded bases, which are most frequently found on the phyllopodia and which tend to detach easily (*Fig. 13*). There is a definite stalk or short flange which attaches to the rhizome in a slight epidermal depression. Peltate scales are generally considered more advanced than subpeltate or other unmodified ones (Bower 1923, p. 200).

*Scale margin.*—The scale margin may be entire, or bear papillae or hairs, or be flabelloid (see the separate discussions on hairs and



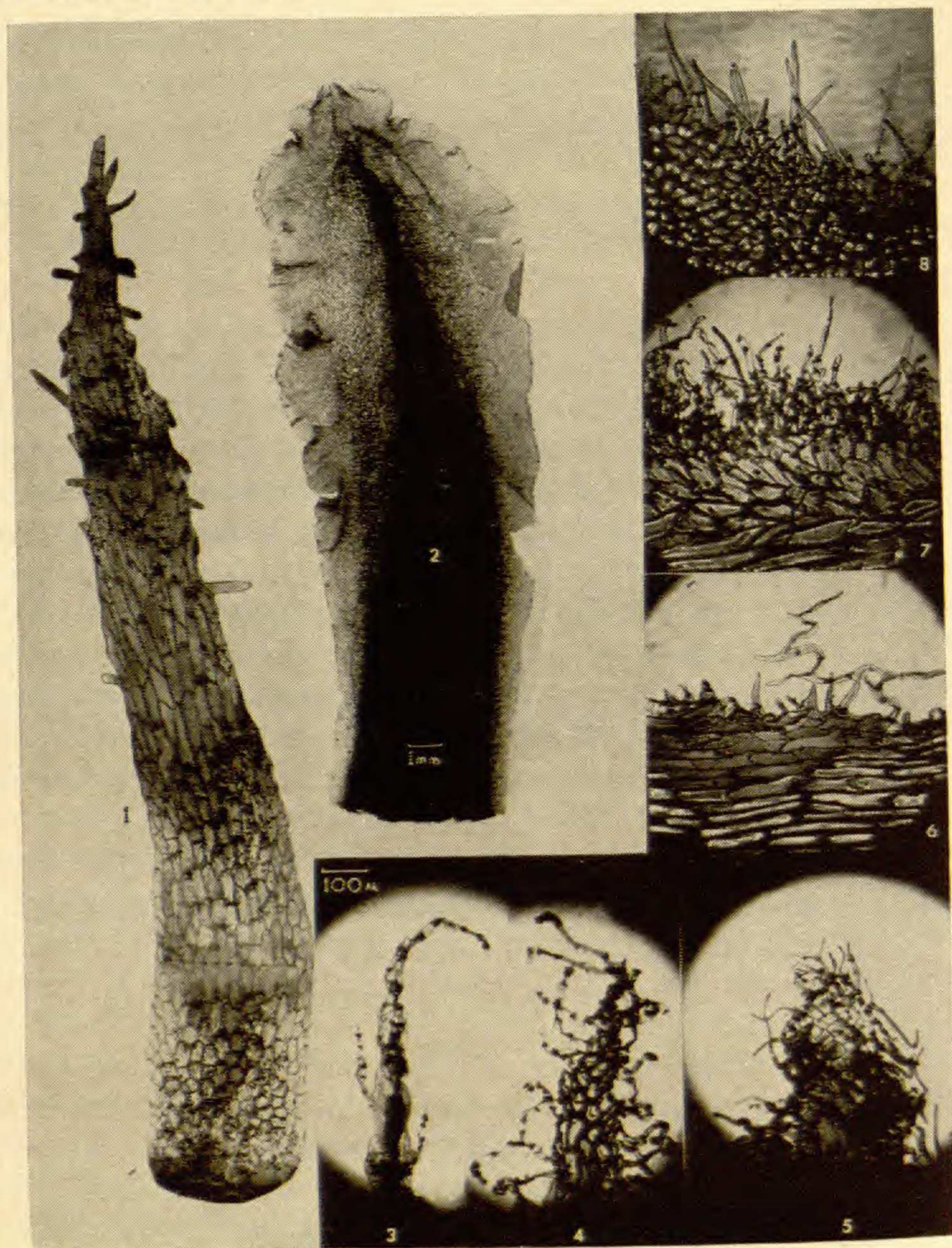
flabelloid margin). Small, dark protuberances are sometimes seen on or near the walls of the marginal cells of *P. grande*, *P. wandae*, and *P. bifurcatum*. They seem to be persistent cell nuclei which have not deteriorated, for in the younger parts of the scale nuclear stains bring out obvious nuclei which if examined in progressively older cells move toward the wall and appear as the small dark protuberances.

*Bicolorous scales*.—The central middle to basal areas of the scale are marked by a stripe on at least some scales of most species. The stripe is composed of cells which have all thickly pigmented brown to black walls. A scattering of lighter colored cells with only their lateral walls thickened may be found among the darker cells. As there is considerable inconsistency in color and pattern of these stripes, it is difficult to use these to evaluate phylogenetic trends. The stripe extends to or nearly to the apex in members of the *P. bifurcatum* group more frequently than in other species. *Platycerium grande* often lacks a well defined stripe, particularly on the larger scales of the phyllopodia.

*Scale development*.—Rhizome scales begin their development from uniseriate hairs. These hairs divide longitudinally, transversely, and clinally at the thickened center to form the scale. For cell details see *Figure 1*. In non-peltate scales the enlargement of the base is by transverse and longitudinal cell division. Peltate scale development in *P. hillii* often shows a cupping in or turning under of the basal auricles, which are eventually obliterated by thickening, enlargement, and overtopping growth of the whole basal area, resulting in a thick, rounded base (*Fig. 13*). The attaching cells that were between the auricles become submarginal and differentiate into a short flange or well-defined stalk. This scale development is similar to that illustrated for *Pyrrosia* (Nayar, 1961, *figs. 7-15*, p. 166), except that there are no auricles.

*Hair distribution*.—Hairs are found on all scales except those of *P. wallichii*. All others have hairs along the edge of the scales; the hairs are sparse near the basal edge. *Platycerium bifurcatum* and *P. hillii* tend to have long, tangled hairs near the apical margin of the scales, but this is not always consistent (*Fig. 4*).





PLATYCERIUM RHIZOME SCALES. FIG. 1. *P. ANGOLENSE*, YOUNG SCALE, GENERALIZED EXCEPT FOR HAIRS. FIG. 2. *P. CORONARIUM*, MATURE SCALE, SPECIALIZED, MARGIN PAPERY, FLABELLOID. FIG. 3. *P. VEITCHII*, FILIFORM APEX. FIG. 4. *P. HILLII*, ACUTE APEX. FIG. 5. *P. GRANDE*, BLUNT APEX. FIG. 6. *P. HOLTUMII*, MARGIN WEAKLY FLABELLOID. FIG. 7. *P. WANDAE*, MARGIN FLABELLOID. FIG. 8. *P. GRANDE*, MARGIN STRONGLY FLABELLOID.

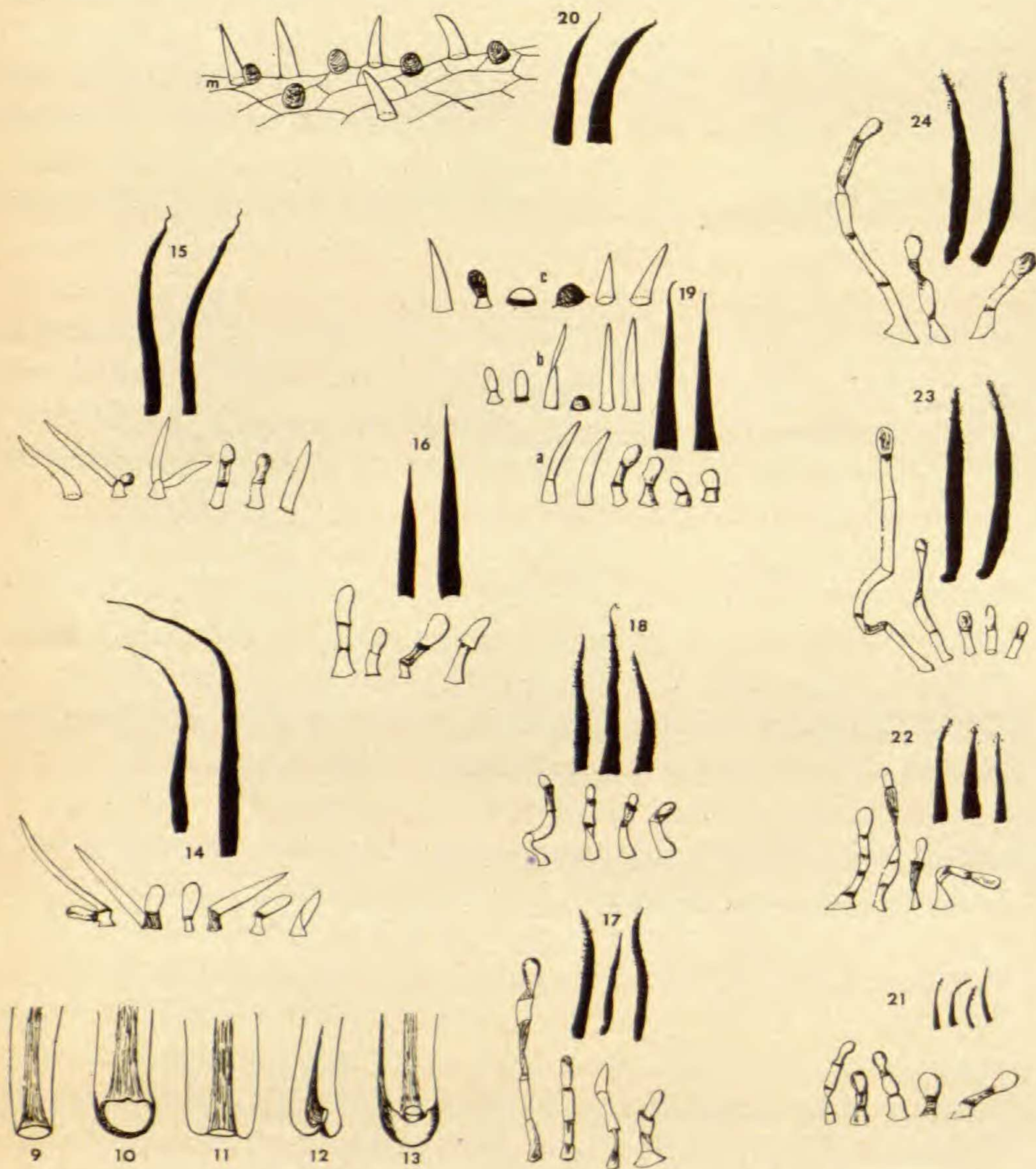


Hairs on the broad surfaces of the scales are found near the apex occasionally in *P. angolense*, and over much of the surface in *P. ellisii* and *P. vassei* (but more sparsely in the latter), and on the face of the marginal cells in *P. ridleyi*. The dense marginal fringe of hairs in *P. holttumii*, *P. wandae*, and *P. grande* scales (Figs. 6-8) arises from marginal and submarginal cells of the flabelloid margin. Having the hairs consistently scattered over the surface of the scale or spreading to a submarginal position occurs in most advanced to moderately advanced species and is to be regarded as more specialized than having hairs limited to marginal cell edges. In the apparently related genus *Pyrrosia*, a similar distribution of hairs is also found among the advanced or moderately advanced species (Nayar, 1965, p. 13).

*Hair types.*—The hairs found on the rhizome scales fall into three intergrading types: glandular, ray, and basic. The glandular types are typically stout, round at the apex, and contain a dark, gland-like substance. The ray types appear much like the rays of the stellate hairs of the lamina; most are whitish and blunt to pointed at their apex, and generally flat, although some are conical and often a bit darker. Basic hairs are close to the ray type in appearance and color, but are typically bent, twisted, or crooked, and not as flat and white as the ray type. Shorter basic hairs bear a close resemblance to the marginal papillae, whereas longer ones may be setiform. Typical glandular hairs are found in *P. ridleyi* (Fig. 30), typical ray types in *P. vassei* (Fig. 19B), and basic types in *P. grande* (Fig. 28B). Some basic types may blend into the ray type, a common condition in *P. wandae* (Fig. 27). All three kinds of hairs and their intermediates are found in the Malayan-Asiatic line (Figs. 25-30). The Javan-Australian line (Figs. 21-24) and the more primitive members of the Afro-American line (Figs. 16-18) have mostly basic to glandular types. Basic to glandular intermediate hairs tend to have the contents of the cell collapsed, causing a distortion of the cells (Fig. 17).

*Origin of the hair types.*—The presence of hair-like papillae and their similarity to basic hairs suggest that basic hairs are derived from elongate papillae. This follows the dictum that trichomes





PLATYCERIUM RHIZOME SCALES AND HAIRS. FIGS. 9-13. RHIZOME SCALE BASES, NOT TO SCALE. FIG. 9. *P. STEMARIA*, BROAD ATTACHMENT. FIG. 10. *P. VASSEI*, BROAD ATTACHMENT, SCALE BENT. FIG. 11. *P. WANDAE*, SUBCORDATE BASE. FIG. 12. *P. WILLINCKII*, SUBPELTATE BASE. FIG. 13. *P. HILLII*, PELTATE BASE. FIGS. 14-30. RHIZOME SCALES AND HAIRS SHOWING CHANGES ALONG EVOLUTIONARY LINES. FIGS. 14-20. AFRO-AMERICAN LINE. FIG. 14. *P. ANDINUM*. FIG. 15. *P. ANGOLENSE*. FIG. 16. *P. STEMARIA*. FIG. 17. *P. QUADRIDICHOTOMUM*.



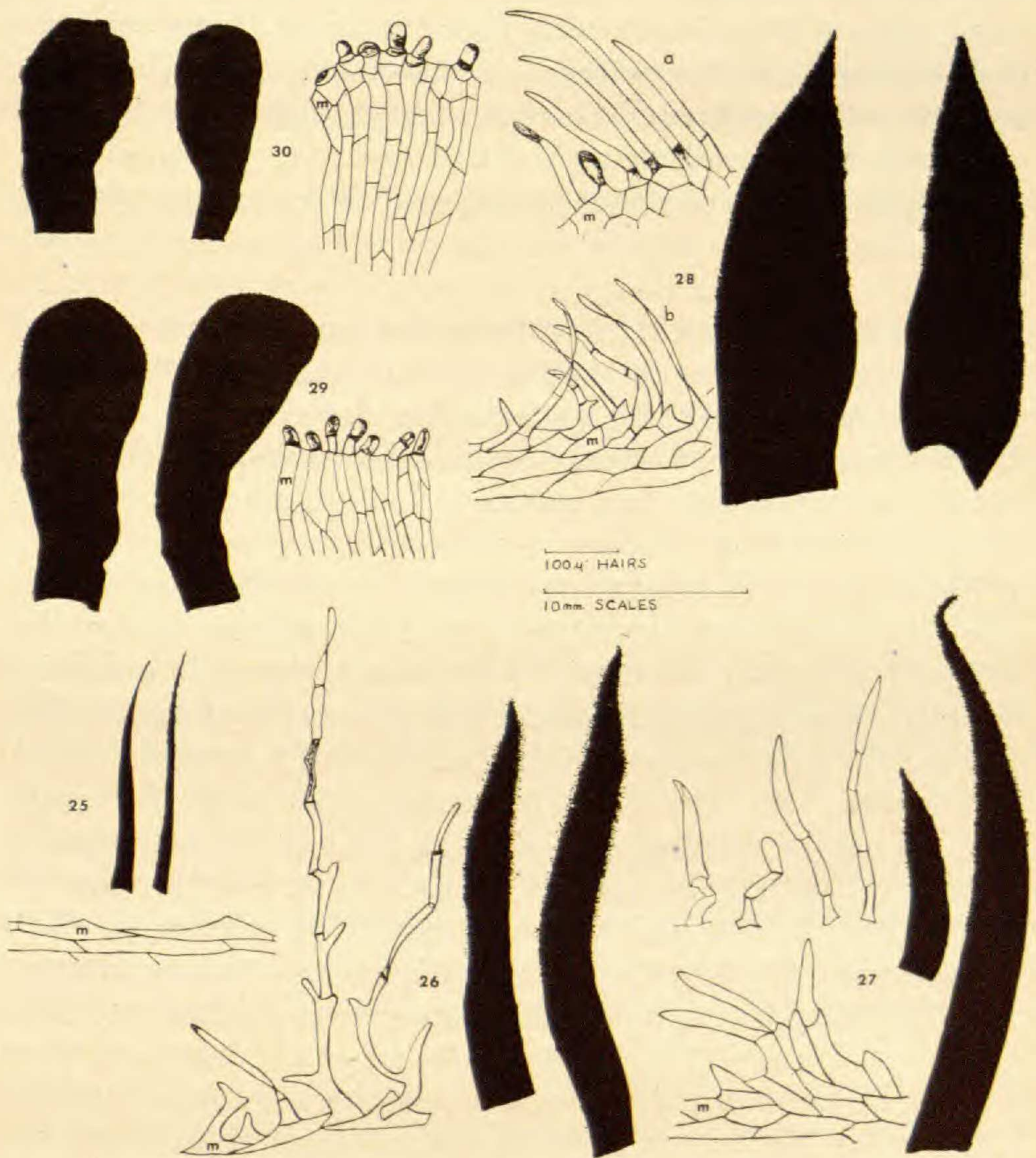


FIG. 18. *P. MADAGASCARIENSE*. FIG. 19. *P. VASSEL*. A, MOZAMBIQUE; B, MADAGASCAR; C, CULTIVATED. FIG. 20. *P. ELLISII*. FIGS. 21-24. JAVAN-AUSTRALIAN LINE. FIG. 21. *P. WILLINCKII*. FIG. 22. *P. VEITCHII*. FIG. 23. *P. BIFURCATUM*. FIG. 24. *P. HILLII*. FIGS. 25-30. MALAYAN-ASIATIC LINE. FIG. 25. *P. WALICHII*. FIG. 26. *P. HOLTUMII*. FIG. 27. *P. WANDAE*. FIG. 28. *P. GRANDE*. A, HAIRS FROM MEDIAL MARGIN; B, HAIRS FROM BASAL MARGIN. FIG. 29. *P. CORONARIUM*. FIG. 30. *P. RIDLEYI*. The abbreviation is: M = MARGINAL CELLS.



originate from papillate epidermal cells (Netolitzky cited in Carlquist, 1961, p. 34). This hypothesis is supported by the presence in *P. holttumii* and *P. grande* of very short to long papillae intermingled with basic hairs, which are distinct only by the cell wall separating the hair cell from the trichoblast.

Uniseriate hairs are generally regarded as the basic type from which many other variants are derived (Wagner, 1964, p. 90). The origin of the glandular hair is from the basic hair. There are all degrees of gradation between these two types. Also, well defined glandular hairs appear only in the more advanced members of the Malayan-Asiatic (*Figs. 29, 30*) and Afro-American (*Figs. 14, 15, 19, 20*) lines and hence correlate with other advanced traits. The Javan-Australian line has retained the intermediate basic to glandular hairs (*Figs. 21-24*).

The origin of ray hairs is not so clear. In the Malayan-Asiatic line they seem to be derived from the basic type or one tending toward a glandular condition; there are all degrees of gradation between these types in *P. grande* and *P. wandae* (*Figs. 27, 28*). In the Afro-American line the ray hairs are often stouter, conical, and seem to have been derived from glandular hairs. These rays may appear as branches off a glandular hair in *P. angolense*, *P. andinum* (*Figs. 14, 15*), and occasionally in *P. vassei*, or may be independent but intermingled with glandular hairs in *P. ellisii* and *P. vassei* (*Figs. 19, 20*). Occasional hairs intermediate between the glandular and the ray condition may be found near the basal margin in *P. vassei*. The abundance of conical ray hairs also seems to indicate an intermediate condition between glandular and ray hairs. When the contents of the conical ray hair collapse, the ordinary ray with its flat shape is produced. Conical ray hairs are mostly found in the Afro-American line, and basic hairs are mostly absent from it. In *P. ellisii*, the ray hairs tend to originate from the center of the trichoblast cell, rather than from one side, as is frequently the case with hairs close to the basic type in origin. Nayar (1965, p. 13) has described hairs on *Pyrrosia obovata* which seem to be similar in many ways to the ray hairs of *Platynerium ellisii*. *Pyrrosia heteractis*, with the basic type of hair, is considered



by Nayar primitive in relationship to *Pyrrosia obovata*. Nayar implied that the hairs which arise from the center of the cell and have dilated bases as in *P. obovata* are separate entities not related to protuberances in origin. It seems that hairs of this type in *Platycerium* are a result of cell reduction or failure of the basal developing hair cell to elongate properly. Similar dilated hair bases on glandular hairs may be found in some forms of *P. vassei* and in *P. ridleyi*.

*Unicellular to multicellular hairs.*—Most of the species have hairs with 2–4 cells. But one has only protuberances known as papillae (*Fig. 25*), others have mostly 1-celled hairs (*Fig. 20*), and others have mostly multicellular hairs (*Fig. 26*). It is generally believed that unicellular hairs are more primitive than multicellular hairs unless the unicellular condition is shown to be a reduction (Netolitzky, cited in Carlquist, 1961, p. 34). In the Malayan-Asiatic line of the genus the primitive *P. wallichii* (*Fig. 25*) lacks hairs and has only papillae which presumably gave rise to 1-celled hairs. Hairs with more cells have evolved, and those of *P. holttumii* (*Fig. 26*) have 8 cells. The next species, *P. wandae* and *P. grande* (*Figs. 27, 28*), show a decrease in the number of cells to 5 or fewer. Basic hairs are still present, but semi-specialized hairs (i.e. intermediate glandular and ray types) have appeared. It seems that the appearance of semi-specialized to specialized hairs may be correlated with at least the partial loss of the basic hair types. In *P. coronarium* (*Fig. 29*), an advanced species, the cells in the hair are reduced to 2 and are glandular. The more advanced *P. ridleyi* (*Fig. 30*) has a large percentage of 1-celled glandular hairs. This reduction trend is also found in the Afro-American line, culminating in *P. ellisii* (*Fig. 20*) which bears only 1-celled glandular or ray type hairs. It also seems that the advanced condition for specialized hairs is from many to few cells.

*Incomplete stellate hairs.*—Ray cells are unicellular (*Fig. 19b*) or are found as terminal or subterminal cells on basic or glandular hairs (*Fig. 14*). Two to several ray cells may appear on the apical cell of a basic or a glandular hair (*Fig. 15*); this condition approaches the stellate hair. A less specialized development pro-



duces a long cell with many lateral ray-like cells along its axis; such hairs are occasionally found on fibrils.

There seems to be a relationship between the stellate hairs found on the lamina and those on the rhizome scales. Rhizome scale hairs apparently show ontogenetic stages no longer present in the development of laminar stellate hairs. The development as studied by Straszewski (1915, p. 277) shows that a laminar stellate hair starts as a glandular cell which divides apically into successive glandular cells that elongate and flatten into rays. By studying a variety of hairs on *P. angolense* scales it is possible to reconstruct a plausible sequence of cell arrangement that could have led up to the stages described by Straszewski.

One might take the point of view that the hairs on the rhizome scale represent reductions from the stellate condition. This seems unlikely, for the cells of a reduced hair would probably be comprised of the component cells of the stellate hair type, i.e. ray and glandular cells. Instead, a continuous array of basic to specialized types of cells are present. Also, if reduction were the case, the most primitive species would have retained more of the stellate hair structure. This is not the case, however, for the species having this condition are not among the very primitive ones.

The stellate hair tendency in scales is best developed in *P. angolense* and *P. andinum*. The other species have other specializations or have not reached the stellate state. The separation of the ray and glandular cells into independent hairs is one type of specialization and is found in *P. ellisii* (Fig. 20).

*Flabelloid margin*.—The cells of the scale margins are generally arranged longitudinally, but may be oriented at various angles, and may even be retrorse (Figs. 2, 28). Margins with cells that spread outwards in a fan-like manner Holttum (1957, p. 43) described as flabelloid. Flabelloidly arranged cells may be absent, in clusters, or continuous, well developed or barely so, and they may merge with papillae and trichoblasts.

If cells bearing protuberances, trichoblasts, and basic hairs are essentially similar and if they can unite laterally to each other in varying degrees, it is possible to explain the origin of the flabelloid



margin by lateral fusion of "free" marginal cells. This hypothesis is likely because there is no difference in color and texture between "free" marginal cells and those making up the flabelloid margin, the marginal cells being united in varying degrees up to a typical flabelloid state, and the orientation of the cells in the flabelloid margin being in the same direction as that of "free" hairs. That marginal cells as well as submarginal cells of a flabelloid margin may continue to produce papillae and hairs is further evidence that the cells of the flabelloid margin are basically the same as the marginal cells of unmodified scales. If the "free" hairs on a flabelloid margin unite, a very broad, flabelloid margin as found in *P. coronarium* and *P. ridleyi* is formed (*Fig. 2*). The cells of these broad, flabelloid margins are oriented like many of the "free" marginal hairs in *P. grande*. In summary, the trend in the Malayan-Asiatic line seems to be from marginal cells arranged longitudinally to a narrow flabelloid margin with many "free" hairs to a wider flabelloid margin with few "free" hairs. This trend is absent or poorly developed in the other evolutionary lines of the genus. Where it does appear it is found in advanced species (*P. vassei* from Madagascar, *P. bifurcatum*, and *P. hillii*).

*False branching.*—False branching occurs in *P. holttumii* (*Fig. 26*) and occasionally in *P. grande*. It is characterized by having one or more hair cells with protuberances. Occasionally the protuberances are separated from the cell by a wall, and then a truly branched condition exists. False branching may be interpreted as a stage toward the fusion of hair cells to form a flabelloid margin. An alternative explanation is that these relatively newly derived basic hairs are still genetically close to the marginal cells and have retained their tendency to form papillae or, alternately, false branches. This seems to be the more adequate explanation, as many of the false branches are not distinct from the papillae of marginal cells.

#### FUNCTION OF THE RHIZOME SCALES

The most vulnerable part of these sometimes immense plants is the relatively small apical bud. Death of the bud results in death



of the whole plant in species which do not produce lateral buds or buds from the roots. Rhizome scales function to protect the bud from desiccation, animals, and excessive water. Beneath the base fronds old rhizome scales may be found very much intact, covering and protecting the rhizome, although the softer parts of the scales may be worn away leaving only the sclerified stripes.

Protection from desiccation is particularly important in these usually high epiphytes, as they are exposed to more drying conditions than low epiphytes or terrestrial plants. I do not know what animals might attack these plants in their native habitats, but the mass of base fronds is known to be a home for a multitude of organisms. Sowbugs, pillbugs, snails, and slugs are capable of eating through the scales and into the buds, particularly on young plants in cultivation. Small insects would probably have difficulty breaking through the scales covering the bud. I have observed scale insects unable to feed because they were entangled in the hairs of the rhizome scales. The insects were able to attach and feed where the rhizome scales ended on the phyllopodia. Smaller animals, however, could gain entry to the bud and rhizome through the injury inflicted by larger animals or microorganisms. The small larvae of fungus gnats (*Mycephilidae*) apparently gain entry to the rhizome bud through leaf scars which are perhaps softened by decay or do not suberize well. Termites, birds, and various fungi also have been observed to make their home in the nest fronds as well.

The base fronds usually form a ruffle of tissue over the bud, which diverts the flow of water. Although this ruffle may be said to serve other purposes, it also helps to keep the bud free of excess water. I believe that keeping excess water off the bud tissue is a very important function of the rhizome scales as well. Waterlogged tissues are particularly vulnerable to microorganism infections. If softened areas are produced from such infections, other organisms then readily find their way into the remaining tissue. The glandular hairs and large amounts of oil found in the rhizome scales of *P. bifurcatum*, *P. grande* (Joe, 1964, p. 71), and probably other species must also play some role in rhizome protection.



## DISCUSSION

With a knowledge of the rhizome scale characters described above and their distribution among the 17 species, it is possible to infer the kind of scales most likely possessed by the ancestral plant. In *Table I*, *P. wallichii* has the lowest value for specialized rhizome scale characters and probably has scales most closely resembling those of the ancestral plant. The relationships of present day species also may be clarified. For example, the general appearance of the South American species *P. andinum* could place it in any of the three evolutionary lines of the genus, but several rhizome scale characters and other less obvious structures place it closest to the African species. However, of broader interest are the changes in rhizome scale structures that have taken place along with the general evolution of the various species. Some of these changes are limited to a few species, but others are established patterns in this and probably other fern genera.

The following changes which have taken place in rhizome scales of *Platycerium* seem to be correlated with evolution in the genus: fibrils present to absent; width narrow to broad; texture firm to thin papery, at least as a broad margin; apex filiform to non-filiform and multicellular; base broadly attached to subpeltately to peltately attached; hairs restricted to the scale margin to spreading submarginally or centrally; margins mostly with papillae to mostly with basic hairs to mostly with typical rays and/or glandular hairs; hairs absent or basic hairs mostly 1-celled to basic hairs multicellular; simple glandular or ray hairs with many cells to the same with few cells; simple hairs to partly formed stellate hairs; and marginal cells oriented with the length of the scale to flabelloid to very broad flabelloid.

From the rhizome scale characters having phylogenetic value the following generalizations are made:

1. Elaborate scale structure is indicative of advanced species, except where reduction of the hair cells is involved.<sup>3</sup>

---

<sup>3</sup> A similar conclusion is reached by R. M. Tryon, Jr., who finds that *Cyathea* scales with the least cellular differentiation are primitive (*in litt.* Sept. 8, 1969).



2. Except in very primitive species, reduction in number of hair cells of simple but not stellate hairs is apparently correlated with increased hair specialization.

3. Hair development on some rhizome scales seems to reflect stellate hair ontogeny and shows stages now absent from the leaf.

4. The flabelloid margin seems to have developed from the union of papillae, trichoblast, and hairs.

5. Peltate scales developed by the folding under of the auriculate or rounded base and subsequent overtopping growth, rather than by the lateral union of the auricles. This is similar to the formation of peltate scales in *Pyrrosia*.

6. One of the important functions of the rhizome scale may be to protect the bud tissue from becoming water-logged.

It seems that greater use may be made of rhizome scales in determining relationships within other genera, providing sufficient features are available. Scale interpretations will be more reliable with some prior knowledge of at least some of the relationships in the group. The use of scale characters will be of greatest help in interpretation of problematic taxa and in reinforcing or supporting other phylogenetic interpretations.

#### LITERATURE CITED

- BOWER, F. O. 1923. The Ferns, vol. I. 359 pp. University Press, Cambridge.
- CARLQUIST, S. 1961. Comparative Plant Anatomy. 146 pp. Holt, Rinehart, and Winston, New York.
- HOLTTUM, R. E. 1957. The Scales of Cyatheaceae. Kew Bulletin 1: 41-45.
- JOE, BARBARA. 1964. A Review of the Species of *Platyserium* (Polypodiaceae). *Baileya* 12: 69-126.
- NAYAR, B. K. 1961. Studies in Polypodiaceae, VII: *Pyrrosia*. J. Indian Bot. Soc. 40: 164-186.
- NAYAR, B. K. and S. CHANDRA. 1965. Ferns of India-XV, *Pyrrosia*. Bull. Nat. Bot. Gard., Lucknow 117: 1-98.
- STRASZEWSKI, H. R. 1915. Die Farngattung *Platyserium*. Flora 108: 271-310.
- WAGNER, W. H., JR. 1952. The Fern Genus *Diellia*, its Structure, Affinities, and Taxonomy. 167 pp. Univ. Calif. Publ. Bot. 26(1): 1-212.
- WAGNER, W. H., JR. 1964. The Evolutionary Pattern of Living Ferns. Bull. Torrey Bot. Club 21: 86-95.

LOS ANGELES CITY COLLEGE, LOS ANGELES, CALIFORNIA 90029.